

SPATIAL AND TEMPORAL DISTRIBUTION OF LARVAL STRIPED MULLET (*MUGIL CEPHALUS*) AND WHITE MULLET (*M. CUREMA*, FAMILY: MUGILIDAE) IN THE NORTHERN GULF OF MEXICO, WITH NOTES ON MOUNTAIN MULLET, *AGONOSTOMUS MONTICOLA*

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ABSTRACT

We determined the seasonality, distribution, and abundance of mullet larvae primarily from Southeast Area Monitoring and Assessment Program (SEAMAP) ichthyoplankton surveys of the northern Gulf of Mexico between 1982 and 1986. Although potentially nine species of mullet can occur in the southern portion of the study area, we found only *Mugil cephalus*, *M. curema*, and *Agonostomus monticola*. *Mugil cephalus* >6 mm SL are separated from *M. curema* and *A. monticola* by total number of anal fin elements. Larval *A. monticola* are separated from *M. curema* >7 mm SL by having a longer caudal peduncle and pigment on the second dorsal fin at about 13.5 mm SL. *Mugil curema* and *M. cephalus* lack pigment on the second dorsal fin until >25 mm SL. Overall, most *M. cephalus* larvae are collected at stations with surface water temperatures $\leq 24.7^{\circ}\text{C}$ (mean: 23.0°C) and salinities $\geq 34.0\text{‰}$; most *M. curema* larvae are collected at stations $\geq 24.5^{\circ}\text{C}$ (mean: 26.3°C) and $\geq 29.9\text{‰}$. During August 1984, we also found 196 *A. monticola* (3.6–25.5 mm SL, N = 8 stations) at surface water temperatures of $28.6\text{--}29.5^{\circ}\text{C}$ and salinities of $28.5\text{--}35.9\text{‰}$; we took all larval *A. monticola* along or west of $93^{\circ}00'$. Adults of all three species of mullet migrate offshore to spawn over or beyond the outer continental shelf. Larval *M. cephalus* are collected from October to March, but are most abundant during November and December. *Mugil curema* are collected primarily from April through September but are most abundant during April–May and to a lesser extent August–September; limited spawning occurs during July. *Mugil* spp. larvae >4.0 mm of both species are collected primarily near the surface. We suggest that based on prevailing current patterns, tag return, and electrophoretic data, *M. cephalus* spawned in the vicinity of the Mississippi River delta during late fall and early winter help maintain mullet populations in the eastern and western Gulf of Mexico.

Nine species of mullet occur in the west-central Atlantic Ocean (Thomson, 1978): striped mullet (*M. cephalus*), white mullet (*M. curema*), dwarf mullet (*M. curvidens*), hospe mullet (*M. hospes*), parassi mullet (*M. incilis*), liza (*M. liza*), fantail mullet (*M. trichodon*), bobo mullet (*Joturus pichardi*), and mountain mullet (*Agonostomus monticola*). Robins et al. (1991) consider *M. trichodon* an extra-limital species not found in waters along the continental United States and include *M. gaimardianus* (redeye mullet) and *M. gyrans* as valid species, assigning the common name fantail mullet to *M. gyrans*. *Mugil cephalus*, *M. curema*, *M. gyrans*, and *A. monticola* occur in the Gulf of Mexico, with *M. liza*, *M. gaimardianus*, and possibly *M. trichodon* along south Florida but more common in the West Indies and southward (Rivas, 1980). Mulletts are of interest worldwide because of their economic importance and potential for aquaculture (Thomson, 1966; Nash and Koningsberger, 1981). Historically, the striped mullet fishery in the gulf has been centered off Florida where mullet are sold fresh or smoked. Roe is also exported to Asia. A striped mullet fishery has also developed off Louisiana and Mississippi since about 1980 and focuses on roe export to Asian markets (Render et al., 1995). Although the striped mullet fishery is one of the most important of those conducted for coastal pelagic fishes (Rivas, 1980), few studies have been conducted in the gulf on striped or white mullet early life history (Arnold and

Thompson, 1958; Caldwell and Anderson, 1959; Moore, 1974; Finucane et al., 1978). Because of increased fishing pressure which targets gravid females prior to spawning, mullet may be susceptible to overfishing; therefore, the need for management-related biological data are great. Thus, our objectives are to provide fishery-independent data on the spatial and temporal distribution and relative abundance of striped mullet and white mullet in the Gulf of Mexico; to provide new information on and discuss characters for separating young *Agonostomus* from *Mugil*; and to discuss an observation by Rivas (1980) that "young or adult mullet occurring along the Florida gulf coast could have been spawned off Louisiana, Mississippi, or Alabama."

MATERIALS AND METHODS

We examined samples taken during Southeast Area Monitoring and Assessment Program (SEAMAP) surveys of the Gulf between 1982 and 1986¹ for larval and juvenile mullet. Standard ichthyoplankton survey techniques as outlined by Smith and Richardson (1977) were employed in data collection. Stations sampled by National Marine Fisheries Service (NMFS) vessels were arranged in a systematic grid of about 55-km intervals. NMFS vessels primarily sampled waters >10 m deep. Plankton tows were made with a 60-cm bongo net (0.333-mm mesh) hauled-obliquely from within 5 m of the bottom or from a maximum depth of 200 m. A flowmeter was mounted in the mouth of each net to estimate volume of water filtered. Ship speed was about 0.75 m·sec⁻¹; net retrieval was 20 m·min⁻¹. At stations <95 m deep, tow retrieval was modified to extend a minimum of 10 min in clear water or 5 min in turbid water. Tows were made during both day and night depending on when the ship occupied the station. Each cooperating state had its own sampling grid and primarily sampled their coastal waters. Overall, 1,829 bongo net tows were taken during these years. We also examined 814 neuston samples taken during SEAMAP surveys from 1982 through 1984. Samples were collected with an unmetred 1 × 2-m neuston net (0.947-mm mesh) towed for 10 min at each station. During April and May, SEAMAP collections were taken primarily beyond the continental shelf in conjunction with NMFS annual larval tuna surveys. Sampling during March, and from June through November was conducted primarily over or immediately adjacent to the shelf. No samples were collected during January and February. Distribution of neuston net collections were similar to that of bongo collections both spatially and temporally. Additional information on temporal and spatial coverage of SEAMAP plankton surveys are found in Stuntz et al. (1985), Thompson and Bane (1986a, 1986b), Thompson et al. (1988), and Sanders et al. (1990). Specimens were preserved in formalin and transferred to 70% ethyl alcohol. We also examined 311 1 × 2-m neuston-net collections (0.947-mm mesh, 10-min tows) from riverine/oceanic frontal zones off the Mississippi River delta for larval and juvenile mullet. These frontal zone collections were made by personnel of NMFS, Panama City, Florida, and contributed 27.6% of all neuston samples examined. Sampling date and number of samples collected were as follows: May 1988 [55 samples]; August 1988 [71]; September 1986 [46], 1987 [68], and 1989 [35]; and December 1988 [36].

Latitude 24°30'N was the southern boundary of the study area in the eastern gulf, a cutoff which approximates the continental shelf break (i.e., 180 m depth contour) along the southern tip of Florida; 26°00'N was the southern boundary of our survey area in the central and western gulf. Longitude 81°00'W was the eastern boundary and the Texas coast the western boundary (Appendix Fig. 1). We divided the gulf into three approximately equal geographic regions based on area (i.e., sq km; Appendix Fig. 1). The eastern gulf was between 81°00' and 87°00'W, the central gulf was from 87°00' to 92°00'W, and the western gulf was west of 92°00'W. We combined seasons as follows: spring (March to May), summer (June to September), and fall/early winter (October to December). We also divided the gulf into approximately equal geographic areas based on water depth and considered inner shelf waters as ≤40 m deep and outer shelf waters as 41 to 180 m deep; oceanic waters were divided into areas 180 to 1,000 m deep and >1,000 m deep. Delineating distribution and abundance of larvae by region, season, and station depth allows inferences about adult distributions, spawning areas, and spawning times (Houde, 1982).

We based the identification of young mullet on characters taken from the literature (Table 1) and additional characters developed herein. Although this paper was not intended as one of larval development, we discuss characters that separate *Agonostomus* from *Mugil* spp. Characters as outlined by Anderson (1957b) include: 1) number of forks at the tip of the posterior branch of the last dorsal and anal fin ray; 2) number of forks at the tip of the four upper and four lower principal rays of the caudal fin; 3) differences in shape of the margin of the preorbital bone and number of serrations along its edge; and 4) differences in fin ray counts. After initially separating larvae based on number of fin elements and fin position (Table 1), we re-examined mullet >15 mm to confirm the presence or absence

Table 1. Characters for separating larval and juvenile mullet <25 mm SL

Taxa	Total elements		Second dorsal/Anal fin position*		
	Second dorsal	Anal	Near origin	Near mid-fin	Behind mid-fin
<i>Agonostomus monticola</i>	9	12		✓	
<i>Joturus pichardi</i>	10	13	✓		
<i>Mugil cephalus</i>	9	11		✓	
<i>M. curema</i>	9	12		✓	
<i>M. curvidens</i>	9	11	✓		
<i>M. hospes</i>	9	12			✓
<i>H. incilis</i>	9	12			✓
<i>M. liza</i>	9	11	✓		
<i>M. gaimardianus</i>	9	12		✓	
<i>M. gyrans</i>	8	11	✓		
<i>M. trichodon</i>	9	11	✓		

* Position of second dorsal fin origin along anal fin base. Placement of second dorsal fin and anal fin is taken from Thomson (1978) or Menezes (1983).

of *Agonostomus* in samples. Then we worked backward to develop additional characters for separating smaller larvae. We measured larvae of co-occurring *M. curema* (N = 10) and *A. monticola* (N = 7) to quantify characters. Measurements were as follows: caudal peduncle length—from base of last ray of second dorsal fin to posterior margin of hypurals; caudal peduncle depth—vertical depth through base of last ray of second dorsal fin; body depth at first dorsal spine—vertical depth through anteriormost spine of first dorsal fin; snout to insertion of first dorsal spine—distance from tip of snout to insertion of anteriormost spine of first dorsal fin; snout to insertion of second dorsal fin—distance from tip of snout to insertion of spine of second dorsal fin. We followed the nomenclature of Robins et al. (1991). We considered notochord length synonymous with standard length (SL) and record all measurements as mm SL or percent SL. Specimens of *M. cephalus*, *M. curema*, and *A. monticola* were illustrated in Ditty et al. (1996).

Water temperature and salinity data were measured at the sea surface. We used a percent cumulative frequency of $\geq 75\%$ of positive stations to define hydrographic conditions (surface temperature, salinity, and station depth) most often associated with occurrences of mullet larvae. Larval mullet are neustonic, therefore, surface temperature and salinity data adequately represent their relationship to hydrography. An univariate method was used to calculate median, mean, and percent cumulative frequency statistics (SAS Institute, 1985). Estimates of larval density (no. of larvae-100 m⁻³), abundance (no. of larvae under 10 m² of sea surface), and catch (no. of larvae-neuston tow⁻¹) were calculated for each station. Arithmetic mean density, abundance, and catch estimates were calculated by month (Table 2), season (Table 3), and region-season (Table 4). Means were calculated by summing each station density, abundance, or catch estimate and dividing by the total number of stations sampled by category. Months were combined across years because each month was not sampled every year. Larval density and catch estimates for *M. curema* were calculated only between March and September because no *M. curema* were caught during October and only one larva in each of November and December. Larvae >25.5 mm were excluded from analyses although we collected young up to 31.5 mm in neuston tows. We compared relative frequency distribution of stations where young mullet were collected (gears combined) among regions, seasons, depths, and diel period, respectively, by a likelihood ratio Chi-square (G^2 , $\alpha = 0.05$; SAS Institute, 1985). Significant differences were evaluated through orthogonal contrasts. We used a Wilcoxon test to evaluate diel differences in catch and standardized density of *M. cephalus* and *M. curema* ($\alpha \leq 0.05$; SAS Institute, 1985) and included only stations where young were caught in analyses.

RESULTS

Separation of Taxa.—Overall, we examined 2,954 bongo net and neuston net samples but found larvae and transforming young of only *M. cephalus*, *M. curema*, and *A. monticola*. *Mugil cephalus* were separated from *M. curema* by seasonal occurrence and from both *M. curema* and *A. monticola* >6 mm by total number of anal fin elements. Number of elements in the second dorsal fin and fin placement (Table 1) separate *M. gyrans* from the other three species known to occur in the northern gulf. Both second dorsal and anal fin ray counts overlap in co-occurring *M. curema* and *A. monticola* (Table 1); therefore, we examined other

Table 2. Mean density (# larvae/100 m³), mean abundance (# larvae/neuston tow) of larval striped mullet (*Mugil cephalus*) and white mullet (*M. curema*) in the northern Gulf of Mexico. Months are combined across years. Numbers in parentheses are stations where we collected larvae (positive catch stations) over total stations sampled by month. Values represent the arithmetic mean density, abundance, or catch for all stations sampled by month.

Gear	March	April	May	June	July	August	September	October	November	December
<i>Mugil cephalus</i>										
Bongo										
Density	0.0	0.0						0.2	3.8	1.1
Abundance	0.0 (0/144)	0.0 (0/164)						1.4 (6/116)	26.4 (26/110)	11.1 (24/108)
Neuston										
Catch	1.8 (8/13)	0.0 (0/95)						0.0 (0/33)	0.0 (0/3)	9.9 (10/95)
<i>Mugil curema</i>										
Bongo										
Density	0.0*	0.0†	0.0*	0.0†	0.0	0.0*	0.0	0.0	0.0	0.0
Abundance	0.1 (1/144)	0.0* (1/164)	0.3 (11/295)	0.0* (2/354)	0.0 (0/139)	0.1 (4/224)	0.0 (0/172)	0.0 (0/116)	0.0 (0/110)	0.0 (0/108)
Neuston										
Catch	0.0 (0/13)	3.1 (21/95)	1.1 (34/211)	0.7 (33/201)	<0.1 (4/92)	0.1 (10/248)	0.9 (19/153)	0.0 (0/33)	0.3 (1/3)	0.0* (1/95)

* <0.05-100 m⁻³ or under 10 m² of sea surface.

† <0.005-100 m⁻³.

Table 3. Catch data for the northern Gulf of Mexico by species, season, and gear type. Fall (October to December), Spring (March to May), and Summer (June to September). Density (# larvae/100 m³); Abundance (# larvae under 10 m² of sea surface); Catch (# larvae/tow). Values represent the arithmetic mean density, abundance, or catch for all stations sampled by category.

	<i>Mugil cephalus</i>			<i>Mugil curema</i>		
	Fall	Spring	Summer	Fall	Spring	Summer
Bongo						
Total Stations	334	603	892	334	603	892
Total Positive Stations	56	0	0	0	11	6
Mean Density	1.7	0	0	0	<0.1*	<0.1†
Mean Abundance	12.8	0	0	0	0.2	<0.1‡
Number of larvae	1,018	0	0	0	21	5
Neuston						
Total Stations	131	319	694	131	319	694
Total Positive Stations	10	8	0	2	55	71
Mean Catch/Tow	7.2	<0.1§	0	<0.1	1.7	0.4
Number of larvae	942	23	0	2	536	303

* 0.02 larvae·100 m⁻³, † 0.003 larvae·100 m⁻³, ‡ 0.03 larvae under 10 m², § 0.07 larvae/tow, || 0.02 larvae/tow.

characters to separate larvae of these two species. Differences in location and amount of guanine on the abdomen and laterally along the body help separate larvae of *M. curema* and *A. monticola* by about 5 mm. In *A. monticola*, guanine was heavier on the operculum, visceral mass, and ventro-laterally along the body than above the body midline. Early larvae of *M. curema* have a much reduced but generally silver-sheen over the entire body.

Length of the caudal peduncle separated larval *A. monticola* from *M. curema*

Table 4. Mean abundance (# larvae under 10 m²) and catch (# larvae/tow) of young mullet by region and season for the northern Gulf of Mexico. Spring (March to May); Summer (June to September); Fall (October to December). Mean abundance is calculated by including all stations sampled by region and season. Numbers in parentheses are stations where we collected larvae over total stations sampled.

	Eastern		Central		Western	
<i>Mugil cephalus</i>						
Bongo						
Spring	0.0	(0/143)	0.0	(0/383)	0.0	(0/77)
Summer	0.0	(0/238)	0.0	(0/359)	0.0	(0/295)
Fall	0.9	(4/57)	4.7	(32/228)	64.4	(20/49)
Neuston						
Spring	0.1	(2/91)	<0.1*	(6/190)	0.0	(0/38)
Summer	0.0	(0/115)	0.0	(0/399)	0.0	(0/180)
Fall	0.4	(3/20)	9.6	(5/97)	0.4	(2/14)
<i>Mugil curema</i>						
Bongo						
Spring	0.1	(3/143)	<0.1†	(5/383)	0.8	(5/77)
Summer	<0.1‡	(1/238)	<0.1§	(1/359)	<0.1	(4/295)
Fall	0.0	(0/57)	0.0	(0/228)	0.0	(0/49)
Neuston						
Spring	<0.1#	(2/91)	1.3	(34/190)	7.6	(19/38)
Summer	<0.1**	(2/115)	0.6	(43/399)	1.5	(26/180)
Fall	0.0	(0/20)	<0.1	(2/97)	0.0	(0/14)

* 0.06 larvae under 10 m², † 0.09 larvae under 10 m², ‡ 0.02 larvae under 10 m², § 0.003 larvae under 10 m², || 0.07 larvae under 10 m², # 0.04 larvae/tow, ** 0.02 larvae/tow.

>7 mm. Caudal peduncle length averaged 19.1% (range: 17.8–20.8%, 7.3–19.2 mm) in *A. monticola* and 15.5% (range: 14.0–16.9%, 5.7–25.0 mm) in *M. curema*. Differences in the number of upper and lower secondary caudal rays and presence or absence of pigment on the second dorsal fin separated *Agonostomus* from *Mugil* by 13.5 mm. Melanophores were present along the base of the second dorsal fin rays of *A. monticola* at about 13.5 mm, with pigment added outward as larvae grew. *Mugil cephalus* and *M. curema* do not have pigment on the second dorsal fin until 25 mm or larger. In addition, transforming *Agonostomus* have 9 or more upper and lower secondary caudal rays whereas *Mugil* spp. have 8 or fewer rays.

In general, *A. monticola* were more slender than *M. curema* but body measurements overlap. Body depth at the first dorsal spine averaged 22.6% (range: 21–25%) in *A. monticola* and 24.7% (range: 23–27%) in *M. curema*. Differences in placement of the anteriormost spine of the first and second dorsal fins and the relationship of the second dorsal fin to the anal fin base among taxa were not significant. The anteriormost spine of the first dorsal fin was inserted near mid-body in *M. cephalus* (mean: 52.0% SL), *M. curema* (mean: 53.0% SL), and *A. monticola* (mean: 51.5% SL). The second dorsal fin originated between 70% and 75% of SL in *M. cephalus*, *M. curema*, and *A. monticola*. In addition, a vertical line through the base of the spine of the second dorsal fin consistently passed thru the sixth or seventh element of the anal fin in all three species. This placed the origin of the second dorsal fin above the middle of the anal fin base. In *M. gyrans*, the second dorsal fin originates over the anterior 25% of the anal fin (Table 1).

Spatial and temporal distribution.—*MUGIL CEPHALUS*. A total of 1983 striped mullet larvae were collected during the study. Larval striped mullet were taken in 56 of 334 bongo net samples during fall, with about 92.5% of larvae ≤ 5.0 mm; 93.7% of young striped mullet from neuston tows were between 4.0 and 10.0 mm. Spawning began during October and was completed by March, with larvae most abundant during November and December (Table 2). We found larvae most abundant overall in the western gulf (Table 4) as was the relative frequency of positive stations ($G^2 = 20.676$, $P \leq 0.001$). Densities exceeded 25 larvae·100 m⁻³ at four stations, all west of Southwest Pass of the Mississippi River (Appendix Fig. 1A). The largest single density estimate (181.8 larvae·100 m⁻³) was at a station off western Louisiana, 185 km south of the Mermentau River (103 m deep, 28°00'N, 93°00'W) during December (Appendix Fig. 1A). Mean catch-tow⁻¹ was greatest in the central gulf (Table 4), due primarily to a single, large neuston collection of 877 striped mullet during December 1983 (Appendix Fig. 1A). This single collection contributed 93% of all striped mullet taken in neuston tows during fall. Mean surface water temperature when spawning began in October was 26°C, declining to 20°C in December. Overall, young striped mullet were collected primarily at stations where water temperatures were $\leq 24.7^\circ\text{C}$ (median: 23.0°C, mean: 23.4°C, range: 16.7–27.0°C) and salinities were $\geq 34.0\text{‰}$ (median: 35.8‰, mean: 34.4‰, range: 23.5–36.8‰) (Fig. 1). Striped mullet were taken at stations between 7 and 2,837 m deep (median: 88 m; mean: 415 m), with the highest relative frequency of positive stations between the 41 and 180 m isobaths ($G^2 = 12.054$, $P \leq 0.001$). Differences in density, catch, and the frequency distribution of positive stations between diel periods were not significant.

MUGIL CUREMA. We caught 867 white mullet during this study, with 98.5% taken in surface collections. All 27 white mullet collected in bongo net tows were < 5.0 mm; 82.2% of white mullet caught in neuston net tows were between 5.0 and 15.0 mm. White mullet began to spawn during March based on the collection of

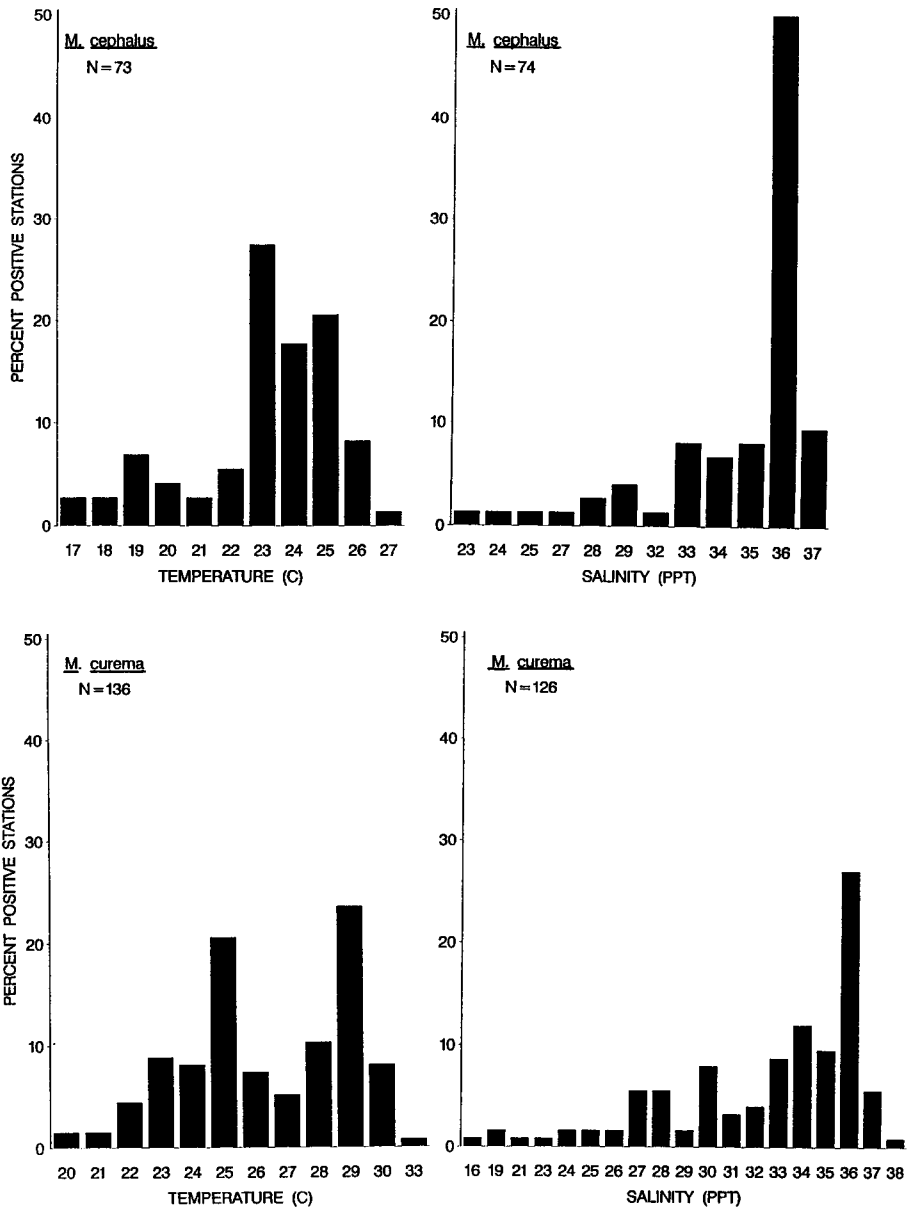


Figure 1. Summary of surface water temperature ($^{\circ}\text{C}$) and salinity (‰) data for larval striped mullet (*Mugil cephalus*) and white mullet (*Mugil curema*) in the Gulf of Mexico. Bongo and neuston net data are combined. Discrepancies in number of stations (N) by taxa are the result of missing hydrographic data. Values are rounded to the nearest whole number.

two-6 mm larvae (Fig. 2). Larvae were most abundant during April–May and to a much lesser extent August–September, with apparently little spawning during July (Table 2, Fig. 2). In addition, the relative frequency of positive stations was significantly higher during spring than summer ($G^2 = 8.48$, $P \leq 0.004$). Spawning was completed by mid-September because all 134 white mullet larvae caught

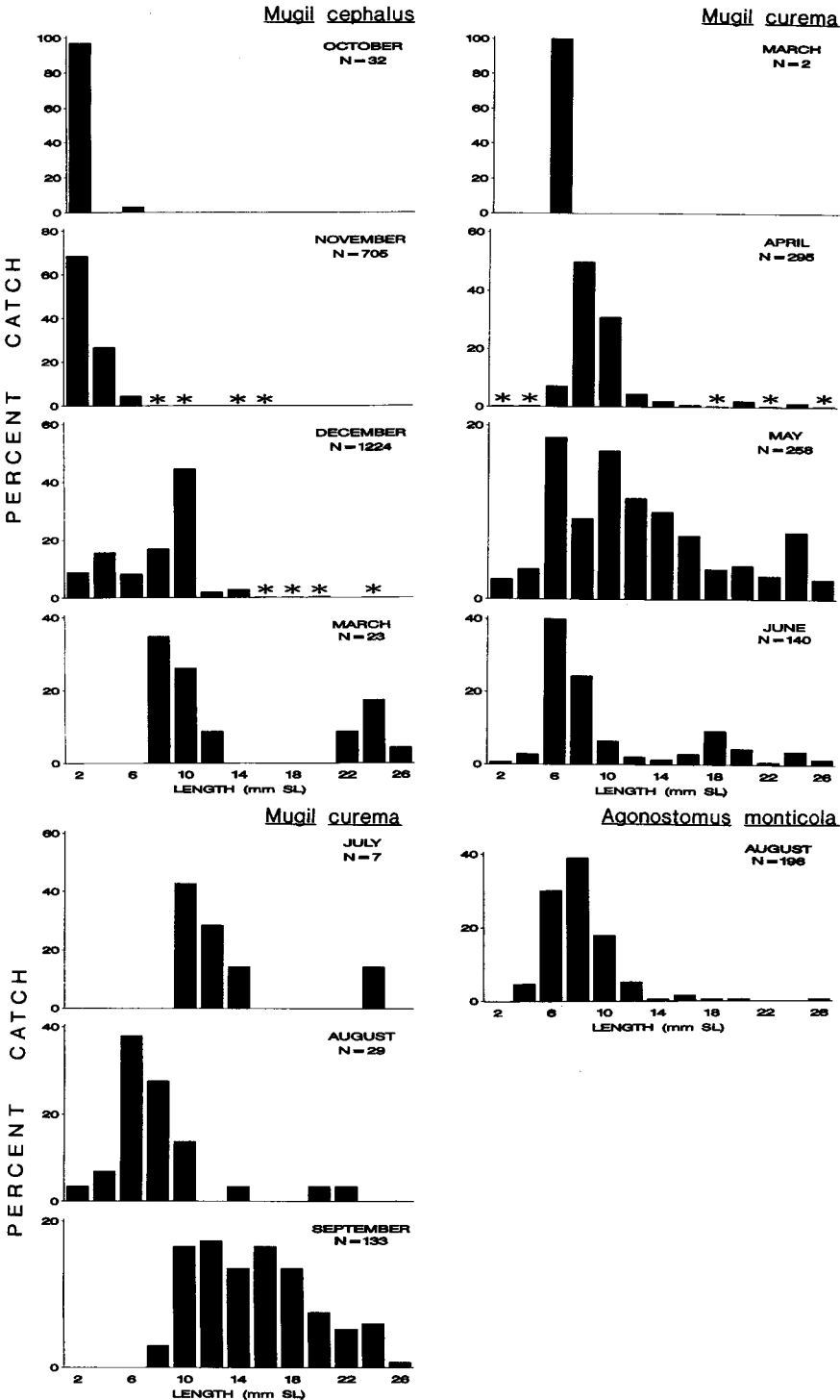


Figure 2. Monthly length-frequency of striped mullet (*Mugil cephalus*), white mullet (*Mugil curema*), and mountain mullet (*Agonostomus monticola*) in the Gulf of Mexico. N = number of larvae. Bongo and neuston net catches are combined. Lengths are rounded to the nearest whole number and combined by 2-mm length intervals. Asterisks indicate catch is <0.5% for given length category.

were ≥ 7.5 mm (Table 2, Fig. 2). We collected only one white mullet during November (15.0 mm; station depth 1,058 m; 27°30'N, 90°30'W) and one during December (24.0 mm; station depth 2983 m; 27°00'N; 87°01'W). These two white mullet were probably spawned during late September or early October. Mean catch/tow (Table 4) and the relative frequency of stations where we caught white mullet were greatest in the western region ($G^2 = 26.043$, $P \leq 0.001$). Catch exceeded 50 larvae-tow⁻¹ in only 2 of 128 positive neuston collections, both in April off south Texas, at stations >1,500 m deep (Appendix Fig. 1B). One collection contained 105 larvae and the other collection 51 larvae. Larval white mullet were taken in 17 of 1495 bongo samples during spring and fall but density estimates never exceeded 3 larvae-100 m⁻³ at any station.

Mean surface water temperatures when spawning began were $\geq 22.0^\circ\text{C}$. Overall, 75% of white mullet were taken at stations where surface water temperatures were $\geq 24.5^\circ\text{C}$ (median: 26.0°C, mean: 26.3°C, range: 20.3–32.8°C) and salinities were $\geq 29.9\text{‰}$ (median: 34.0‰, mean: 32.5‰, range: 16.5–37.5‰) (Fig. 1). In addition, we collected white mullet at stations between 11 and 3,111 m deep (median: 100 m; mean: 550 m). The relative frequency of positive stations during spring was highest between the 41 and 180 m isobaths ($G^2 = 17.479$, $P \leq 0.001$). During summer, however, when larvae were less abundant, we found a higher frequency of positive stations between the 181 and 1000 m isobaths ($G^2 = 6.314$, $P \leq 0.012$). In addition, we found 38 of 43 white mullet between 25.0–31.5 mm at stations >200 m deep. Diel differences in density, catch, and the frequency distribution of positive stations were not significant; however, white mullet were more common in neuston tows during day than night ($P \leq 0.07$).

AGONOSTOMUS MONTICOLA. We collected 196 mountain mullet (3.6–25.5 mm; $N = 8$ stations; Fig. 2) during this study. All mountain mullet were caught in the western gulf (along or west of 93°00'W) during mid-August 1984 (Appendix Fig. 1D), and all but one larva in neuston tows. Surface water temperatures were between 28.6 and 29.5°C and salinities ranged from 28.5 to 35.9‰ (median: 35.6‰, mean: 33.8‰); stations were between 26 and 1,336 m (median: 78 m) deep.

DISCUSSION

The seasonality of larvae separates *M. cephalus* from *M. curema*. In addition, total number of anal fin elements separate *M. cephalus* from *M. curema* and *A. monticola* >6 mm. A shorter caudal peduncle and pigment on the second dorsal fin separate *M. curema* from *A. monticola* by 7 mm and 13.5 mm, respectively. Differences in amount of guanine between taxa are difficult to quantify and some silver coloration may have faded during preservation. We believe, however, that differences in guanine concentration help separate taxa and are not related to storage, preservation, or other unknown factors. Other characters that distinguish *Mugil* spp. and *Agonostomus* are often incompletely developed until about 15–20 mm or larger. For example, the presence or absence of forking at the tip of the last dorsal and anal fin rays, and four upper and lower principal caudal rays is indistinct until >15 mm. In addition, fin rays are easily broken during collection, preservation, and handling, which compounds the difficulty of using this character. Differences in the shape of the posterior margin of the preorbital bone and extent of serrations along its front edge also separate taxa (Anderson, 1957b), but these differences are indistinct until about 20 mm. Furthermore, the third anal spine does not transform until 30–40 mm in *M. curema* and not until 35–45 mm in

Table 5. Comparison of overall mean density (# larvae/100 m⁻³) and mean abundance (# larvae under 10 m² of sea surface) of striped mullet, *Mugil cephalus*, in the Gulf of Mexico. Gear type is 60-cm bongo nets.

Study	Mesh size (mm)	Tow type	Month/Year	Mean density	Mean abundance	Total # stations sampled	Study location
This study	0.333	Oblique	Nov*	3.8	26.4	110	Gulfwide
			Dec*	1.1	11.1	108	
Fruge (1977)	0.505	Oblique	Nov, 1974	—	33.7	49	Off Louisiana
Houde et al. (1977)	0.505	Oblique	Jan, 1973	—	8.3	51	Off Florida
Finucane et al. (1977)	0.333	Double	Nov, 1976	1.9	21.2	7	Off south Texas
		Oblique	Dec, 1976	19.8	239.9	7	
Finucane et al. (1979)	0.333	Double	Jan, 1976	0.6	6.7	16	Off south Texas
			Nov, 1977	0.8	7.8	7	
		Oblique	Dec, 1977	3.6	39.0	7	

* Month is combined across years (1982–1986) and regions.

M. cephalus (Anderson 1957a, 1958). Thus, the number of anal spines does not allow separation of *Mugil* from *Agonostomus* until >30 mm.

We found young *M. cephalus* from October through March, with peak spawning during November and December (Table 2) as have other studies (Table 5). The majority of spawning occurs at stations over or beyond the outer continental shelf when surface temperatures drop below 25°C (Fig. 1; Appendix Fig. 1A). An upper limit for spawning of about 25°C agrees with Nash et al. (1974) who found that water temperatures ≥25°C results in >90% egg mortality.

Young *M. cephalus* occur most frequently and are more abundant at stations in the western region (Table 4), although striped mullet are common at stations along both the Texas and Louisiana outer shelf (Appendix Fig. 1A). Higher density and abundance estimates overall in the western than central region may be a reflection of our regional cutoff at 92°00' which roughly divides Louisiana in half (Appendix Fig. 1). For example, we found three of the four largest densities and the largest individual catch of young *M. cephalus* at stations in the central region. The fourth station is off western Louisiana and in the western region (Appendix Fig. 1A). Densities at these four stations are similar to those of Fruge (1977) who found concentrations of striped mullet larvae at two locations west of the delta, one of which extended southwestward from Southwest Pass of the Mississippi River. Concentrations of mullet larvae in the vicinity of the delta are consistent with those found in other frontal areas (Kingsford and Suthers, 1994). Mean monthly densities we found off Texas are comparable to those of other gulf surveys (Table 5), with the exception of a high density estimate during December 1976 (Finucane et al., 1977), resulting from a large collection of larvae at the outermost station of their seven station transect. Spawning apparently occurs near Finucane et al.'s (1978) outer station because of a similarly large estimate of *M. cephalus* eggs and larvae in the same area during December 1977. Waters off Florida are not as well-sampled during peak *M. cephalus* spawning times; however, the small number of larvae collected in the eastern Gulf by Houde et al. (1979) and during this study is surprising given the abundance of adult *M. cephalus* in that region. We found only 16 *M. cephalus* larvae in 57 bongo net and 20 neuston net tows of the eastern region during fall. Houde et al. (1979) took only 10 *Mugil* larvae during November (from 167 bongo collections over a three year period) and 49 larvae during January.

The number and length of *M. cephalus* larvae we collected during March (N = 23, all >7.8 mm; Fig. 2) suggest that offshore spawning is complete by late-

February, which agrees with adult reproductive data off Louisiana (Render et al., 1995). We did not collect larval *M. cephalus* in extensive sampling of oceanic waters during April and caught only nine striped mullet between 20.0 and 25.5 mm overall. Thus, length-frequency data support previous findings that most young *M. cephalus* leave offshore waters by April and move shoreward, first appearing on outer beaches along the U.S. Atlantic and Gulf of Mexico coasts at about 20.0–25.0 mm (Gunter, 1945; Kilby, 1955; Anderson, 1958; Springer and Woodburn, 1960; Sabins, 1973; Rogers and Herke, 1985). The influx of immigrants moving into estuarine areas and bays begins during November and peaks during January–February (Gunter, 1945; Kilby, 1955; Anderson, 1958; Springer and Woodburn, 1960; Sabins, 1973; Rogers and Herke, 1985).

We found *Mugil* larvae >4.0 mm of both species near the surface as have other field studies (Eldridge et al., 1977; Powles, 1981; Collins and Stender, 1989). In addition, we caught generally more *M. curema* in surface nets during day than night ($P \leq 0.07$) as did Eldridge et al. (1977) and Collins and Stender (1989). We did not collect *M. cephalus* in surface nets until December. This may be a sampling artifact since bongo net tows (226) outnumbered neuston tows (36) by six to one during October and November (Table 2). However, >90% of *M. cephalus* collected during October and November were ≤ 4.0 mm (Fig. 2) and may not have been retained by the 0.947 mm mesh of neuston nets. Differences in vertical distribution may also account for larvae <4.0 mm not being available to neuston tows. Although *M. cephalus* spawn near the surface (Arnold and Thompson, 1958), larvae sink during two critical growth periods 2–3 days and 7–8 days posthatch (Kuo et al., 1973), exhibiting strong positive phototaxis at >3.5 mm (Liao, 1974). Since larvae reared in the laboratory at 22°C are 3.5 mm total length (TL) at 10 days post-hatch (Kuo et al., 1973), larvae <3.5 mm may not be available to surface-towed nets during the aforementioned two critical periods. Differences in vertical distribution and behavior of early *M. cephalus* larvae require further study.

We found young *M. curema* primarily from April through mid-September, which agrees with previous ichthyoplankton surveys (Anderson, 1957a; Powles, 1981; Ditty et al., 1988; Collins and Stender, 1989), and with gonad maturation data (Moore, 1974). Initiation of spawning coincides with rising water temperatures during early spring, with peak spawning during late March and April (Table 1; Finucane et al., 1977; 1979). Limited spawning occurs during July based on bimodal length classes (Fig. 2), supporting reproductive information for *M. curema* that suggest an interrupted spawning season (Moore, 1974; Collins and Stender, 1989).

We found *M. curema* primarily over or beyond the outer shelf (Appendix Fig. 1), as did Collins and Stender (1989). Houde et al. (1976), however, found white mullet eggs in Biscayne Bay, Florida, which suggests that some spawning also occurs in inshore waters. We found no clear pattern of shoreward movement with growth as has been suggested for *M. curema* along the Atlantic coast (Anderson, 1957a; Collins and Stender, 1989). In fact, we found a significantly higher proportion of positive stations during summer between the 181 and 1,000 m isobaths. In addition, we found 88% of our 25.0–31.5 mm *M. curema* in waters beyond the shelf break, suggesting some early juvenile white mullet may utilize offshore waters as a nursery area. *Mugil curema* are reportedly estuarine-dependent and young are collected along beaches and in outer bays during late April, with immigration to estuarine areas continuing through August or September (Gunter, 1945; Kilby, 1955; Anderson, 1957a; Richards and Castagna, 1976; Sabins, 1973).

Overall, density estimates are more than an order of magnitude higher and

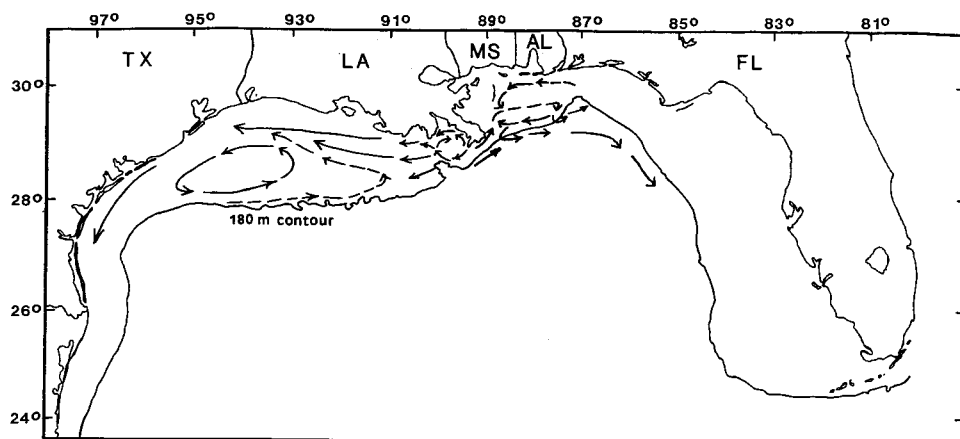


Figure 3. Generalized circulation pattern of the Louisiana-Mississippi-Alabama shelf during fall and winter. Arrows indicate direction of flow; broken lines are subjective. Data are from Murray (1976), Cochrane and Kelly (1986), and Dinnel (1988).

catch/tow about four times greater for *M. cephalus* than for *M. curema* during the season when striped mullet (fall) and white mullet (spring) are most commonly collected (Table 3). The magnitude of these differences support information on adult stock size by Rivas (1980) who found the average annual catch of *M. curema* represents about 2% of *M. cephalus*. Generally low densities of *M. cephalus* and *M. curema* from bongo net tows is not surprising given that mullet are neustonic. For example, Finucane et al. (1977; 1979) found mean densities in neuston tows of 526 larvae and 179 larvae·100 m⁻³ for *M. cephalus* during December 1976 and 1977, respectively. Similarly, density estimates of *M. curema* near the surface ranged from 16.9 larvae to 51.0 larvae·100 m⁻³ during spring (Finucane et al., 1977; 1979). We can not compare densities from surface tows with those of Finucane et al. (1977, 1979) or Collins and Stender (1989) because our neuston tows were unmetered.

Based on an observation by Rivas (1980) that "young or adult mullet occurring along the Florida gulf coast could have been spawned off Louisiana, Mississippi, or Alabama," we examined the distribution of surface currents around the Mississippi River delta as a mechanism for distributing larval *M. cephalus* to other areas of the gulf. Prevailing currents over the inner and middle shelf west of the Mississippi River delta are generally westward most of the year (Cochrane and Kelly, 1986). During fall and winter when *M. cephalus* spawn, currents are along-shore at mean current speeds of 20–30 cm·sec⁻¹ (17–26 km·day⁻¹; Murray, 1976), decreasing to 5–15 cm·sec⁻¹ (4–13 km·day⁻¹) over the west Louisiana shelf (Shaw et al., 1985). The pool of young *M. cephalus* spawned over the middle shelf could either be entrained in the anticyclonic (clockwise) gyre immediately west of the delta (Murray, 1976) and be available to Louisiana estuaries, or be transported west-northwestward towards Texas (Fig. 3) as hypothesized for larval *Brevoortia patronus* (Shaw et al., 1985). Young *M. cephalus* have moved inshore to estuarine nurseries by summer when currents along Texas and western Louisiana reverse and flow towards the northeast (Cochran and Kelly, 1986). Thus, young *M. cephalus* would not be transported back towards Louisiana by this reverse flow.

Outer shelf/slope flow south of the delta is generally eastward most of the year (Murray, 1976; Kelly et al., 1982; Dinnel, 1988). During fall, eastward flowing

currents turn onto the Louisiana-Mississippi-Alabama (LA-MS-AL) shelf forming two counter-rotating circulation cells: an inner-shelf cyclonic (counterclockwise) cell, and an outer-shelf/slope anticyclonic cell (Fig. 3). During winter, the anticyclonic cell is not present and shelf circulation consists of a single cyclonic cell flowing westward over the inner shelf and eastward over the middle shelf. Peak current speeds can exceed $30 \text{ cm}\cdot\text{sec}^{-1}$ ($26 \text{ km}\cdot\text{day}^{-1}$; Dinnel, 1988). Larvae spawned over the inner and middle shelf east of the delta would be retained in the cyclonic gyre off Mississippi Sound and be available to LA-MS-AL estuaries. Larvae spawned over the LA-MS-AL outer shelf/slope would be transported toward the Florida panhandle.

Tag returns indicate that *M. cephalus* along the Florida gulf coast do not make extensive migrations (Idyll and Sutton, 1951; Funicelli et al., 1989). Most remain in a relatively small area (Idyll and Sutton, 1951; Rivas, 1980; Funicelli et al., 1989) and return to their original bay system after spawning (Mahmoudi et al., 1989). In addition, electrophoretic data from populations along both the Atlantic and gulf coasts of Florida suggest that gene flow within and among areas is sufficient to maintain a genetically homogeneous population of *M. cephalus* (Campton and Mahmoudi, 1991). Thus, tag return and electrophoretic evidence is consistent with a hypothesis of a common source of larvae being transported downstream by surface currents from outer shelf spawning grounds. Ocean current patterns off south Florida and in the northern Caribbean may also explain the distribution of *Mugil curema* (Alvarez-Lajonchere, 1976; Powles, 1981) and *M. cephalus* (Collins and Stender, 1989) larvae along the southeastern United States.

Adult *A. monticola* are abundant in freshwater streams and rivers of Puerto Rico, the West Indies, Mexico, and Central and South America (Cruz, 1987; Phillip, 1993), but are apparently rare in the gulf. We found 196 larval and transforming *A. monticola* (3.6–25.5 mm), whereas only three (29–36 mm) are previously recorded from Louisiana (Suttkus, 1956) and Texas waters (Schlicht, 1959). These 196 *A. monticola* represent about 88.5% of all mullet taken during the August 1984 cruise. Fortunately, the August 1984 cruise is one of the most extensive made during the study period, extending from Tampa Bay, Florida, to Corpus Christi, Texas (Appendix Fig. 1D). We found *A. monticola*, however, west of $93^{\circ}00'W$ only. Unfortunately, surface waters of the northern Gulf are poorly sampled from September through December, hindering our ability to more clearly define the spatial and temporal distribution of *A. monticola*. Assuming growth rates for *A. monticola* similar to those for summer-spawned *M. curema* ($15\text{--}20 \text{ mm}\cdot\text{month}^{-1}$; Anderson, 1957b), spawning occurred during July and August. Our findings agree with gonad data which suggest a spawning season from June to October in the Caribbean (Erdman, 1977; Phillip, 1993) but extending to December off Honduras (Cruz, 1987). Spawning through December is also supported by Anderson (1957b) who collected 10 *A. monticola* (24.1–31.3 mm) on cruises during November–December and January–February at six locations off the Bahamas and along the southeastern United States. These specimens, however, may have been spawned farther south and carried northward by prevailing currents (Anderson, 1957b). Our finding of larval *A. monticola* offshore supports Anderson's (1957b) contention that spawning occurs at sea. We examined Mississippi River and Calcasieu River discharge data, tropical cyclone activity, and satellite-images of the western gulf for August 1984, but found nothing to explain the observed station distribution pattern where mountain mullet occurred during that time period (Appendix Fig. 1D). We did not collect larval or juvenile *M. gyrans* although adults occur along the Florida gulf coast. *Mugil gyrans* larvae and juveniles are common in Tampa Bay and south Florida estuaries, but adults may

not migrate offshore to spawn (pers. comm., Mark Leiby, Florida Dept. Natural Resources, Marine Research Institute, St. Petersburg 33712). Length-frequency data suggest that *M. gyrans* are spring–summer spawners (Kilby, 1955; Springer and Woodburn, 1960; Sykes and Finucane, 1966).

In conclusion, little historical information is available on larvae of mullets from the Gulf of Mexico. We provide the first gulf-wide study of young mullet utilizing standard techniques. We also provide early-life data that support findings obtained from juvenile and adult collections and discuss new information on larvae of poorly known mountain mullet which suggests that *A. monticola* may not be as uncommon as previously thought.

ACKNOWLEDGMENTS

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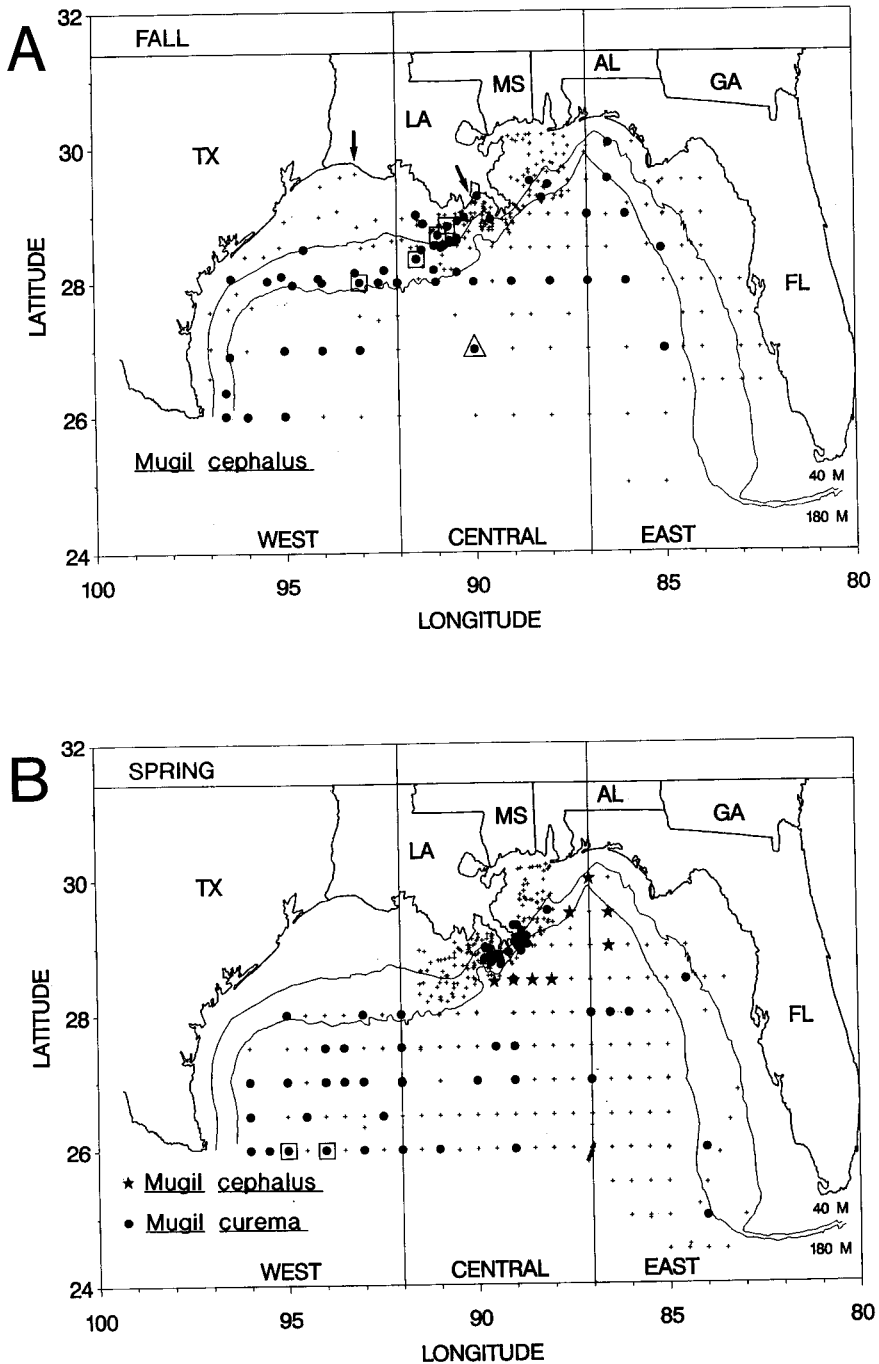
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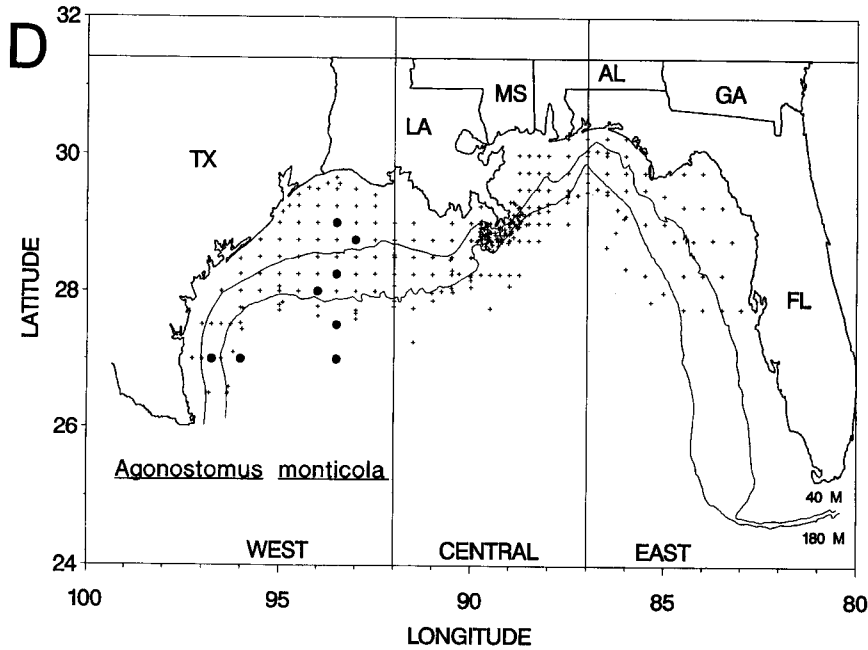
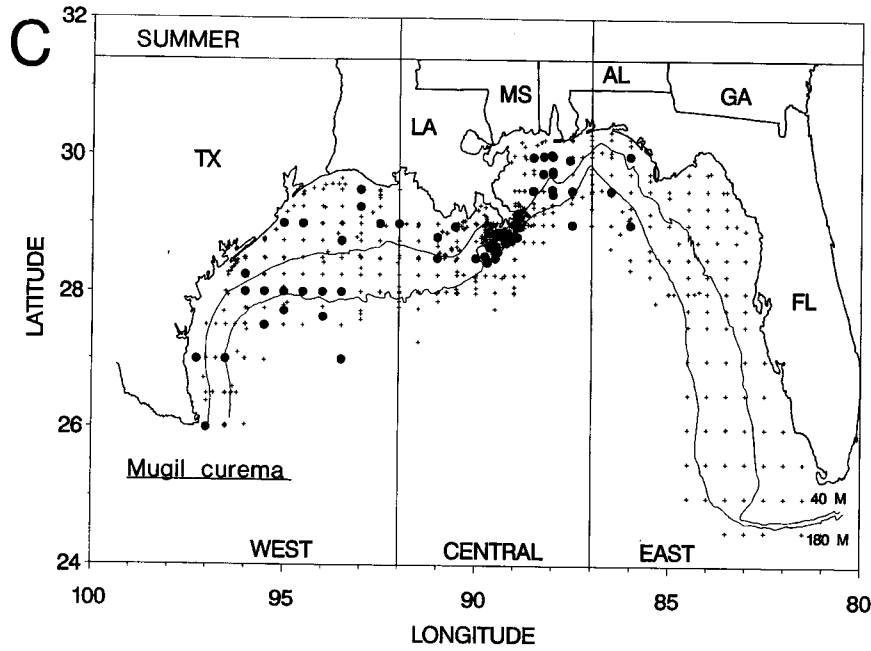
DATE ACCEPTED: March 16, 1995.

ADDRESS: Center for Coastal, Energy, and Environmental Resources, Coastal Fisheries Institute, Louisiana State University, Baton Rouge, LA 70803 (504) 388-6374, FAX (504) 388-6513.

¹ SEAMAP, 1983–1987. (plankton). ASCII characters. Data for 1982–1986. Fisheries-independent survey data/National Marine Fisheries Service, Southeast Fisheries Center: Gulf States Marine Fisheries Commission, Ocean Springs, MS (producer).



Appendix Fig. 1. Distribution of striped mullet (*Mugil cephalus*), white mullet (*M. curema*), and mountain mullet (*Agonostomus monticola*) in the Gulf of Mexico. A. Stations where striped mullet occurred during fall (October–December). Arrows indicate the location of Caminada Pass (to the east) and the mouth of the Mermentau River (to the west). Hollow triangle is location of station with neuston catch of 877 larvae; hollow squares are density estimates exceeding 25 larvae·100 m³. B. Stations where striped mullet (stars) or white mullet (circles) occurred during spring (March–May). Hollow squares



are locations of stations with neuston catches >50 larvae/tow. C. Stations where white mullet occurred during summer (June–September). D. Distribution of sampling (+) and stations where mountain mullet occurred during August 1984.